Breaking from the cage and taking over an island:
Relentless increase and range expansion of white-winged parakeets in Puerto Rico

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Abstract

Puerto Rico has experienced multiple introductions of Psittaciformes which have established self-sustaining populations, and the white-winged parakeets (*Brotogeris versicolurus*) has been considered the most successful invasive psittacine species in the island. In this study, we evaluated their population size, calculated growth rates and estimated the breeding proportion in two populations by performing roost counts for four consecutive years in addition to evaluating their range expansion. We also assessed their diet and breeding ecology. Population estimates parakeets during the study period showed a steady increase, with a maximum of 3,010 individuals in the San Germán population, and a maximum of 3,128 individuals in the San Patricio population. Both populations exhibited a geometric mean population growth rates of 25% per year. As expected, the data indicates that the populations experienced a lag-phase and prior to growing exponentially. This is supported by the island-wide sighting trends and range expansion. Moreover, we detected range expansion during our study via colonization of new areas. The population estimates and population growth rates, along with the sighting trends and their wide distribution makes the white-winged parakeet the most successful psittacine species in Puerto Rico. The factors leading to their invasion success are likely to include propagule pressure, their diet breath and their capability as primary nesters in termite mounds, which are abundant in the island. Currently, the growth rate of the white-winged parakeet does not appear to be limited by any predator, resources or nest availability, and we expect them to continue increasing and expanding their range.

Key words: biological invasions; birds; *Brotogeris*; islands; population growth; Psittacidae; Puerto Rico

Introduction

Non-native invasive species are viewed as a significant component of global biological change (Vitousek et al. 1996), and often have negative impacts on native species, communities and ecosystems (Luque et al. 2013). Different modes of introduction of non-native species have been identified (Carlton 2003), and most introduced species essentially start with small populations (Sakai et al. 2001). Whether they become invasive (*sensu* Blackburn et al. 2011) or not depends on a myriad of factors (*e.g.*, propagule pressure, Holle and Simberloff 2005, pre-adaptive characters, Sol 2008, and/or facilitation by other species Helms and Vinson 2003). Two main processes characterize invasive species: exponential population growth and range expansion, these often are preceded by a lag-phase (Sakai et al. 2001). Understanding the link between population growth and range expansion may help in developing management strategies for invasive species.

Birds are among the most widely introduced taxonomic group across the world (Blackburn et al. 2009). Several modes of introductions have been responsible for avian introductions, *e.g.*, accidental releases (Blackburn et al. 2009) and releases by acclimatization societies (Eguchi and Amano 2004; Duncan et al. 2006). Additionally, in recent times, the pet trade is one of the most common modes of introduction of invasive bird species (*e.g.*, Russello et al. 2008; Carrete and Tella 2008; Cassey et al. 2015). Exotic bird species regarded as invasive often show (close-to) exponential population growth and range expansion (Blackburn et al. 2009), with the former serving as a precursor to the latter (Veit 1997). Among birds, Psittaciformes in particular have been favorably and highly traded in the pet market, and as a result, psittacine species are one of

the most successful groups of birds to establish populations outside their native range (Cassey et al. 2004).

Perhaps the most widely known invasive species of psittacines are the monk parakeet (*Myopsitta monachus*) and the rose-ringed parakeet (*Psittacula krameri*). As with invasive birds in general, invasive populations of monk parakeets in the USA and Spain have exhibited exponential growth, with an estimated population growth of 15% (between 1972–1995; van Bael and Pruett-Jones 1996), and 8% (Domènech et al. 2003), respectively. In the USA, even after a control program attempt, both the abundance and range of monk parakeets were increasing exponentially (Blackburn et al. 2009). Similarly, rose-ringed parakeets exhibit exponential population growth and aggressive range expansion has been recorded (Nebot 1999; Butler 2003; Kleunen et al. 2010; Dodaro and Battisti 2014).

Puerto Rico has experienced perhaps the highest rate of introduction of parrots in the wild (Falcón and Tremblay, *in press*), and the white-winged parakeet (*Brotogeris versicolurus*) has been considered the most successful psittacine species established on the island (Pérez-Rivera et al. 1985; Raffaele 1989; Camacho-Rodríguez et al. 1999; Oberle 2000). Although Pérez-Rivera et al. (1985) warned that the white-winged parakeet could expand and cause significant damage to crops, there is no evidence of crop damage yet. Previous surveys has confirmed the persistence of locally common and self-sustaining populations of the white winged parakeet (Pérez-Rivera et al. 1985; Raffaele 1989; Camacho-Rodríguez et al. 1999; Oberle 2000). Since 2004, and 35 years after it was first reported in the wild in Puerto Rico, populations of white-winged parakeets occupy a wide range in the island (Falcón and Tremblay, *in press*). This brought renewed

concerns about the possible negative effects that the parakeet might have on the native flora and fauna if the white-winged parakeet kept expanding its range, and on the agricultural sector.

In this study, we assess the invasive ecology of the white-winged parakeet – including aspects of their population estimates, population growth rates, range expansion, and natural history. In concordance with the wide range of habitats occupied by white-winged parakeet on the island (described by Falcón and Tremblay, *in press*), we expected to find evidence of exponential population growth rates and range expansion. We also address the possible factors that may have contributed to the establishment success of white-winged parakeets in Puerto Rico.

Materials and Methods

Study species

Brotogeris (Psittacidae) is a small genus (7–8 spp.) of abundant Neotropical parakeet species (Juniper and Parr 1998; Forshaw 2010), occupying varied habitats from dry savannas to tropical rain forests (del Hoyo et al. 1997). Some of these species, if not all, have been harvested to supply the demands of the pet trade market, which is likely to have resulted in population reduction in their native habitat, while some of these species have had their populations reduced as a consequence of habitat destruction (e.g., *B. phyrrhoptera*; Birdlife International 2016).

The white-winged parakeet (*Brotogeris versicolurus*) is considered a widespread species in its native range of South America, occupying French Guiana, the Amazon basin from the north of Brazil to the south-east of Colombia, east of Ecuador, north of

Argentina and Paraguay and the south-east of Brazil (Forshaw 1973). Its non-native range includes Ecuador (west of Los Andes, Freile et al. 2012, California Arrowood 1981, and Florida, Juniper and Parr 1998; Forshaw 2010). Moreover, in 1969, Kepler made the first report of feral white-winged parakeets in Puerto Rico, in the area of Luquillo (Bond 1971), and since, others have reported its presence and persistence (Pérez-Rivera et al. 1985; Raffaele 1989; Camacho-Rodríguez et al. 1999). Currently, the white-winged parakeet is considered the most successful psittacine species in Puerto Rico, based both on its distribution and sighting trends (Falcón and Tremblay, *in press*).

The white-winged parakeet is considered mainly a frugivorous species, although they may also use nectar and seeds as part of their diet (Janzen 1981; Pérez-Rivera et al. 1985; Francisco et al. 2002). Many psittacines, including the white-winged parakeet, roost communally (Juniper and Parr 1998; Brightsmith et al. 2017). The white-winged parakeet nests in arboreal termite mounds and sometimes in tree cavities (Pérez-Rivera et al. 1985). Moreover, we observed that in Puerto Rico, a proportion of the roosting population presumably break up into pairs and breed from late December to June and then eventually re-join the non-breeding roosting proportion of the population. This was confirmed by Tossas et al. (2012) in a population in San Germán, Puerto Rico and has also been reported in the native range (Forshaw 1973; Juniper and Parr 1998). In the continental U.S., fledglings have been reported to stay with the parents and return to the roosting sites after the breeding season (Schroads 1974; Arrowood 1981). In California, the parakeets have shown roosting site fidelity (Arrowood 1981), and in Florida, seasonal and annual shifts in roost sites have been reported (Schroads 1974). The birds were not marked in any of the previous studies, so it is impossible to determine if this involves the

same individuals across time (Brightsmith et al. 2017).

Population ecology of the white-winged parakeet

To estimate the roosting population size, we used the Roost Count Method as described in Wunderle (1994); for other examples see: Chapman et al. 1989; Gnam and Burchsted 1991; Pithon and Dytham 1999; Tossas et al. 2012. We identified roosting sites for each population during the non-breeding season, following flocks before dusk. Then we identified areas from which the birds could be readily observed entering or leaving the roosting area. The monitoring period started from dawn in Guaynabo and before dusk in San Germán and stopped after 20 minutes with no birds departing or entering the roost area. Since the birds gather in flocks and fly in different directions from or to the roosting area, each observer counted birds flying out of- or into- the roosting area in different directions to avoid double counting. If any flock returned to- (San Patricio) or left the- (San Germán) roosting area it was subtracted from the count values, as they would ultimately depart from the area again, thus avoiding double counting. We used SLR cameras with telephoto lens (70-300mm) to photograph the flocks and then counted the quantity of individuals for large flocks (>16 individuals) from the photos. Days with bad weather which resulted in difficulty in counting the birds were avoided and counts were repeated if necessary. Non-breeding counts (representing the minimum population size) in the municipality of Guaynabo were conducted in September of each year (2007–2009, but in 2010 it was conducted in November due to rains), and the counts in the municipality of San Germán were conducted in October of each year (2007–2010). In 2010, we performed breeding counts during late March (mid-late breeding season) in

both roosting populations to estimate the proportion of breeding birds. To test the effectiveness of our method with the white-winged parakeet, we conducted three counts spaced a week apart from September to October 2007 in the Guaynabo population.

For estimates of population size and growth rates, we assumed that 1) all the parakeets roosted communally during de non-breeding season and that during the breeding season, only non-reproductive parakeets roosted communally, 2) the parakeets returned to roost in the same area after the breeding season, 3) the counts that were performed during the non-breeding season reflected the population size after mortality and emigration events shortly after the breeding season, and 4) the number of parakeets counted in each roost is accurate, and 5) the estimated population size represents the minimum number of parakeets in the roost.

We calculated the population growth rates using the equation for exponential growth in populations with overlapping generations (Equation 1; Rockwood, 2006) re-arranged as

$r = \ln\left(\frac{N_t}{N_0}\right)/t$ to get the r values, where:

r is the intrinsic rate of increase;

N_t is the population size at time t;

N_0 is the initial population size;

t is the time in years

This model assumes that 1) the population has overlapping generations and that 2) the population exhibits a stable age structure. In this model, the population grows if $r > 0$, decreases if $r < 0$ and is stationary if $r = 0$. We then converted the r values to the finite

rate of increase per year, with the equation $\lambda = e^r$. When $\lambda < 1$ the population decreases, the population is stable if $\lambda = 1$ and the population increases if $\lambda > 1$.

To determine the proportion of the breeding population, we subtracted the number of parakeets counted during the breeding censuses of 2010 from the population estimates of the 2009 non-breeding censuses. Since both adults have been reported to roost in the nest until all the chicks are fledged (Schroads 1974), we divided the total number of breeding individuals by two to get the approximate number of breeding pairs.

To compare the roosting counts with sighting trends across the island, we used observation count reports from *Ebird* for analyzed in Falcón and Tremblay (*in press*). *Ebird* is an open access observational database that provides a base for evidence-based research, conservation and management actions in a cost-effective way, particularly in the absence of scientifically-derived data (Sullivan et al. 2017).

Range expansion of the white-winged parakeets

To assess the range expansion of white-winged parakeets in Puerto Rico, we used historical occurrence locations derived from the literature and *Ebird* used by Falcón and Tremblay (*in press*). We considered, chronologically, each location points as the center of the parakeets' range and assumed a 2.5 km^2 buffer around it. By doing so, all points that fell in the buffer were treated as the same record location, even if these were observations from different years. Consequently, we ended up with a dataset that comprised of the total range per year, allowing us to visualize and calculate range expansion. Due to lack of information on the home ranges of *Brotogeris* parakeets, we assume an area of 1.5 km^2 to be their home range, which is larger than the home range recorded for other parakeet

species (*e.g.*, Robinet and Salas 2008; Strubbe and Matthysen 2011). Therefore, our analysis and parameter estimates should be considered conservative.

Diet and nesting ecology of the white-winged parakeet

During the study period, we made observations on the nesting ecology and diet of the white-winged parakeet in the Metropolitan Area of San Juan. Observations for breeding and nesting activity were made year-round for the first year of this study (2007) and was later concentrated during the months of December-June for each subsequent year because the nesting season coincided with that reported in the invasive range of Florida and in southwest Puerto Rico (Tossas et al. 2012; Brightsmith et al. 2017). Diet observations were made opportunistically upon encountering flocks, and we also extracted data from Pérez-Rivera et al. (1985).

Statistical analyses

We performed all data pre-processing, obtained summary statistics, and visualizations using R ver. 3.3.3 (R Core Team 2017), and packages *ggplot2* for producing figures (Wickham 2016). We mapped occurrence records and visualized distribution results using QGIS ver. 2.18.14-Las Palmas de G. C. (QGIS Development Team 2017).

Results

Population ecology of the white-winged parakeet

We tested the effectiveness of our Roost Count Method by conducting three counts spaced a week apart from September to October 2007 in the Guaynabo population, and

the population estimates exhibited low variability (range: 1,164–1,299 ±72 SD). The San Germán population of white-winged parakeets increased from 1,503 birds in 2007 to 3,010 birds in 2010. However, although the San Patricio population was steadily increasing from 2007–2009, from 1,299 to 3,128 individuals, a population decline occurred in 2010, and the population was reduced to 2,531 individuals (Fig. 1). Both populations exhibited overall positive population growth rates, with a geometric mean λ = 1.24 (±0.48) in San Patricio, and λ = 1.26 (±0.08) in San Germán during the study period (Table 1). If we consider the population estimates prior and after our population estimates (a period of 29 yr in San Patricio, and 40 yr in San Germán), both populations exhibited λs of 1.20 and 1.17, respectively. Moreover, the island-wide sum of the mean counts per municipality shows the same pattern of increase (Fig. 1)

Based on the breeding census, we estimated that 40% of the population at San Patricio was breeding (625 pairs), and 42% of the population at San Germán (512 pairs; Table 2). Based on the number of birds retuning to the roost after the breeding season, the number of fledglings (recruitment) was estimated to be 604 for San Germán (assuming 2 chicks per pair), but because of the population decline, it was not possible to estimate this for the San Patricio population.

Range expansion of the white-winged parakeets

As with the population and sighting trends, range expansion exhibited a lag-phase with a subsequent exponential increase (Fig. 2). The lag-phase took place from ca. 1985–2005, followed with an exponential increase from 2005–2017.

Nesting and diet ecology of the white-winged parakeet

The annual breeding cycle of the white-winged parakeet in the Metropolitan Area of San Juan starts in January, at the end of the dry season, with reproductive pairs starting to inspect possible nests, and continues through February with pairs constructing their nests. They may use new termite mounds, or re-use termite mounds used in previous years for nesting. Between February and April, reproductive pairs nest and raise their chicks while non-reproductive parakeets presumably stay at the roosting sites. Most chicks are fledged by June, and presumably join the roosting parakeets along with their parents. In terms of nesting, although there were tree cavities likely suitable for the white-winged parakeets in some places where nesting occurred, all nest we found were constructed in termite mounds of *Nasutitermes sp.* in native and exotic trees (Table 3). Two nests inspected with a pipe inspection camera early in the breeding season revealed one clutch of three eggs and one clutch of four eggs. Moreover, five nests inspected later in the breeding season with the same method revealed a mean of 2.14 (±0.69 SD) chicks per nest.

White-winged parakeets use mostly exotic species of plants as food resources, and as in their native range, they are primarily frugivorous, but also consume flowers, seeds and sap (Table 3; complimented with data from Pérez-Rivera et al. 1985).
Sixty-eight percent (68%) of species used as food resources were non-native plants (32% were native), 67% of the species used for nesting resources were non-native plants (33% native; most nests were found in termite mounds that occurred on this plant species), and of four plant species used as roosting resources, two were non-native and two were native.

Discussion

In this study, we estimated the size of two populations of white-winged parakeets in Puerto Rico, and assessed their population growth rates, range expansion, and breeding and diet ecology. Moreover, we compared the population dynamics of these two populations of white-winged parakeets with historic data and sighting trends across the island. Overall, we found that (i) the populations of white-winged parakeets showed a sustained population increase over the study period, (ii) exhibited extremely high population growth rates, (iii) a sustained range expansion, (iv) that they mainly use termite mounds for nesting and the breeding phenology of the population in the Metropolitan Area of San Juan coincides with that of the population in San Patricio and populations in Florida (USA), and (v) that they have a wide diet breadth, but rely heavily on exotic species.

Our population size estimate yields results of positive growth rate consistent with those found by (Tossas et al. 2012). Comparing the historic number of parakeets in the study populations with data from this study, and their population growth rates, suggest that the population exhibited a lag-phase, and was growing exponentially by 2010. This is consistent with the data on sighting trends obtained from Falcón and Tremblay (*in press*), and range expansion data.

The resulting population decrease in 2010 was probably due to emigration and the establishment of a new roosting site in the Río Piedras Botanical Garden, where parakeets would forage, but did not roost prior to this roosting splitting event (5.6 km from the San Patricio roosting site). Around 800 parakeets were seen roosting at this new location. If we assume that the parakeets at the new roosting site originated from the San Patricio

population, then a minimum of 200 fledglings were produced (considerably lower than the production in San Germán), and about 300 pairs abandoned the San Patricio roost. Another roosting site was established in 2012 at the University of Puerto Rico, 5.5 km from the San Patricio roosting site, and 1.5 km from the Botanical Garden population.

Migration to and from the roosting sites is a factor that can affect our population growth estimates and bias our results since we are not considering migration and we assume that the changes in populations are due to birth and death rates. Our surveys in the vicinity of both study populations suggested that they were the only existing roosting sites in the areas, a fact that was confirmed by Tossas et al. (2012) for the San Germán population. During our surveys, we were able to detect the establishment of a new roosting site, which probably originated from the San Patricio population, so emigration is a factor regulating population size. Although white-winged parakeets can exhibit yearly variation in terms of the number of individuals at the roost site, the variation is low within the peak of the breeding and non-breeding seasons (Tossas et al. 2012). The emigration events of a proportion of the roost to a new site is likely determined by some density threshold cue or resource limitation close to the roosting site.

The Roost Count Method was evaluated along with Point Transects, Line Transects and mark-recapture by Casagrande and Beissinger (1997), and the four methods produced 95% confidence intervals that overlapped and similar population estimates. Moreover, we tested this method over a three-week period, and the estimates exhibited very low variability. Given this and that we were able to detect the establishment of the new roosting site, which likely explains the population decline in San Patricio, we are confident that our methods and estimates are robust.

Population growth rates of species of birds regarded as invasive are usually exponential, and often exhibit a lag-phase before this exponential growth (Sakai et al. 2001; Blackburn et al. 2009) and we have observed both of these patterns in the Puerto Rican populations of *B. versicolurus*. Although some species may exhibit very rapid population growth and range expansion, many bird species have a tendency of having long lag-phases between the time of initial introduction and later exponential population growth (e.g., collared doves, Isenmann 1990, penduline tit and the Serin finch, Hengeveld 1989). Three main mechanisms have been proposed to explain the lag-phase often exhibited by invasive species: inherent, environmental and genetic (Crooks and Soulé 1999). The inherent lag effect is the expected lag in population growth of founder populations, whether or not they are adapted to the new environment (*e.g.*, using Equation 1, the population grows relatively slowly in absolute numbers, which is depicted by the shallow portion early in the growth curve; *ibidem*). In the case of environmental lag effects, these refer to situations where environmental changes enhance the fitness of the species, and triggers an increase in its growth rate, which would result in longer lag phase than that expected from the inherent lag effect (*ibidem*). Moreover, genetics may cause lag-phases in species as founder populations may lack local genetic adaptions to the abiotic and/or biotic environment, and a period of time may be needed for new genetic combinations to arise via mating, the appearance and spread of beneficial mutations through the population (*inbidem*), and/or the appearance and spread of novel beneficial genotypes as a result of secondary contact between individuals of genetically-distinct populations. Although there is no way of determining what caused the population

lag-phase of the white-winged parakeet in Puerto Rico, and that different mechanisms may have been at play, we believe that food and nesting resource limitation may have been a major cause of a slow population increase. In the late 1990s, ca. 90% of the land in Puerto Rico was used for agriculture, and during the 1940s the economy of Puerto Rico began shifting from agriculture to manufacturing, which resulted in the abandonment of agricultural lands and subsequent development of secondary forests (Grau et al. 2003). Today, forest cover (predominantly woody vegetation) is estimated in 53% (Gould et al. 2008). As a result, we believe that food and nesting (termite mounds) resources used by the white-winged parakeet have increased dramatically, which may have aided in the population increase and range expansion.

Exotic species that exhibit high population growth rates may be more likely to establish viable populations (Ehrlich 1986; Moulton and Pimm 1986; Pimm et al. 1988; Pimm 1989; Cassey 2001). Additionally, as the size of species' population increases, so does the geographic distribution (Veit 1997), so we can expect that population growth will probably result in spread, but not always (Gaston 2003; Gaston et al. 2003; Blackburn et al. 2006). It has been proposed that populations of birds exhibiting a positive population growth rate have a proportional increase in long dispersing individuals (vagrants) to the increase in population size and thus, increasing the chances of the species invading new ranges (Veit 1997; Veit 2000). Our data and observations suggest that the rapid increase and high number of parakeets in the San Patricio population led to the emigration and establishment of new roosts, therefore expanding their range. This is supported by the lag between population increase at the largest roosting sites on the island, and the island-wide population increase (based on sighting

trends; Falcón and Tremblay, *in press*).

The nesting phenology observations in the Metropolitan Area of San Juan are consistent with the findings of the population in San Germán (Tossas et al. 2012), and in Florida (Brightsmith et al. 2017). Moreover, diet observation of the white-winged parakeet coincide with previous reports on the island (Pérez-Rivera et al. 1985), are consistent to those reported elsewhere in their invasive and native range (Brightsmith et al. 2017), and show that although they use native species, the majority of the plant species consumed are exotic ones.

Various factors may have contributed to the recent success of white-winged parakeets in Puerto Rico. Firstly, propagule pressure may have been an important factor leading to the introduction and establishment during the 1960's and 1980's, when these birds were popular and cheap. According to the CITES Trade Database, the main exporter to the USA (and therefore Puerto Rico) was Peru, with 2,832 white-winged parakeets exported in a single shipment in 1985. Secondly, they have a wide diet breath, and make use of common species that are found especially in anthropogenically-modified areas, to which this species' distribution is highly associated with (Falcón and Tremblay, *in press*). Thirdly, because they nest in termite mounds, which are highly abundant in the secondary forests of Puerto Rico and urban areas (especially in parks), white-winged parakeets are not limited by the scarcity of tree cavities as in other parrot species. Fourthly, no predation observation have been noted, suggesting that predation pressure is low, and the potential predator pool is rather small (including *Falco peregrinus*, *F. columbarius*, *F. sparverius*, *Acipiter striatus* and *A. cooperii*; Brightsmith et al. 2017). Fifthly, trapping seems to supply the local (informal) pet market, rather than serving for

exportation, further increasing the parakeet numbers in the wild (Falcón and Tremblay, *in press*).

Based on their wide distribution across the island and sighting trends compared to other species (Falcón and Tremblay, *in press*), their positive growth rates, and ability to successfully colonize new areas, white-winged parakeets can be indeed considered the most successful psittacine species in Puerto Rico. Although concerns have been raised about the possible negative impacts that psittacine species introduced to Puerto Rico may have on the endemic Puerto Rican parrot (*Amazona vittata*) and on the agricultural sector (see Tremblay and Falcón, *in press*, for a discussion), we did not perceive nor believe that white-winged parakeets pose and threat and would engage in such negatives impacts. Finally, the success of this species, as well as their large numbers and distribution present research opportunities for studying population management with conservation application for parrots and parakeets in their native range.

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References

Arrowood PC (1981) Importation and status of canary-winged parakeets (*Brotogeris versicolurus*) in California. In: Pasquier RF (ed) Conservation of New World parrots. Washington D.C, pp 425–429

Birdlife International (2016) *Brotogeris pyrrhoptera.* The IUCN Red List of Threatened Species e.T22685966A93094507. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22685966A93094507.en. Accessed 26 Dec 2017

Blackburn TM, Cassey P, Gaston KJ (2006) Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. Journal of Animal Ecology 75:1426–1439. doi: 10.1111/j.1365-2656.2006.01167.x

Blackburn TM, Lockwood JL, Cassey P (2009) Avian invasions: The ecology and evolution of exotic birds. Oxford University Press

Bond J (1971) Sixteenth supplement to the Check-list of the Birds of the West Indies (1956). Philadelphia Academy of Natural Sciences, Philadelphia

Brightsmith D, Burgio KR, Hiller BJ, et al (2017) White-winged parakeet (*Brotogeris versicolurus*), vers. 3.0., The birds of North America. Cornell Lab of Ornithology. doi.org/10.2173/bna.whwpar.03

. In: Rodewald PG (ed) The birds of North America, 3rd edn. Cornell Lab of Ornithology,

Butler CJ (2003) Population Biology of the Introduced Rose-ringed Parakeet Psittacula Krameri in the UK.

Camacho-Rodríguez M, Chabert-Llompart J, López-Flores M (1999) Guía para la identificación de las aves exóticas establecidas en Puerto Rico. División de Recursos Terrestres, Departamento de Recursos Naturales y Ambientales de Puerto Rico, San Juan

Carlton J (2003) Invasive Species. Island Press

Carrete M, Tella JL (2008) Wild-bird trade and exotic invasions: a new link of conservation concern? Frontiers in Ecology and the Environment 6:207–211. doi: 10.1890/070075

Casagrande DG, Beissinger SR (1997) Evaluation of four methods for estimating parrot population size. Condor 99:445–457.

Cassey P (2001) Are there body size implications for the success of globally introduced land birds? Ecography 24:413–420.

Cassey P, Blackburn TM, Russell GJ, et al (2004) Influences on the transport and establishment of exotic bird species: An analysis of the parrots (Psittaciformes) of the world. Global Change Biology 10:417–426. doi: 10.1111/j.1529-8817.2003.00748.x

Cassey P, Vall-Llosera Camps M, Dyer E, Blackburn TM (2015) The biogeography of avian invasions: History, accident and market trade. In: Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions. pp 37–54

Chapman CA, Chapman LJ, Lefebvre L (1989) Variability in Parrot Flock Size - Possible Functions of Communal Roosts. Condor 91:842–847.

Crooks JA, Soulé ME (1999) Lag Times in Population Explosions of Invasive Species: Causes and Implications. In: Invasive Species and Biodiversity Management. Springer Netherlands, Dordrecht, pp 103–125

del Hoyo J, Elliott A, Sargatal J (1997) Handbook of the birds of the world. Volume 4, Sandgrouse to cuckoos. Lynx, Barcelona

Dodaro G, Battisti C (2014) Rose-ringed parakeet (Psittacula krameri) and starling (Sturnus vulgaris) syntopics in a Mediterranean urban park: Evidence for competition in nest-site selection? Belg J Zool 144:5–14.

Domènech J, Carrillo J, Senar JC (2003) Population size of the monk parakeet (*Myiopsitta monachus*) in Catalonia. Revista Catalana d'Ornitologia 20:1–9.

Duncan RP, Blackburn TM, Cassey P (2006) Factors affecting the release, establishment and spread of introduced birds in New Zealand. In: Allen RB, Lee WG (eds) Biological invasions in New Zealand. Springer-Verlag, Berlin/Heidelberg, pp 137–154

Eguchi K, Amano HE (2004) Spread of exotic birds in Japan. Ornithol Sci 3:3–11. doi: 10.2326/osj.3.3

Ehrlich PR (1986) Which animals will invade? In: Mooney HA, Drake JA (eds) The ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, pp 79–95

Falcón W, Tremblay RL (*in press*) From the cage to the wild: Introductions of Psittaciformes to Puerto Rico. PeerJ.

Forshaw JM (1973) Parrots of the world. Lansdowne Press, Melbourne

Forshaw JM (2010) Parrots of the World. Princeton University Press, Princeton

Francisco MR, Lunardi VD, Galetti M (2002) Massive seed predation of *Pseudobombax grandiflorum* (Bombacaceae) by parakeets *Brotogeris versicolurus* (Psittacidae) in a forest fragment in Brazil. Biotropica 34:613–615. doi: 10.1111/j.1744-7429.2002.tb00582.x

Freile J, Solano-Ugalde A, Salas J, Navarrete R (2012) *Brotogeris versicolorus* (Statius Müller, 1776) (Aves: Psittacidae): introduced established population in Ecuador.

Brotogeris versicolorus (Statius Müller, 1776) (Aves: Psittacidae): introduced established population in Ecuador 8(3):572. doi: 10.15560/8.3.572

Gaston KJ (2003) The Structure and Dynamics of Geographic Ranges. Oxford University Press, USA

Gaston KJ, Jones AG, Hanel C, Chown SL (2003) Rates of species introduction to a remote oceanic island. Proc R Soc B 270:1091–1098. doi: 10.1098/rspb.2003.2332

Gnam R, Burchsted A (1991) Population estimates for the Bahama parrot on Abaco Island, Bahamas. Journal of Field Ornithology 62:139–146.

Gould, W. A., Alarcón, C., Fevold, B., Jiménez, M. E., Martinuzzi, S., Potts, G., et al. (2008). The Puerto Rico Gap Analysis Project Volume 1: Land cover, vertebrate species distributions, and land stewardship. *Gen. Tech. Rep. IITF-39*, *1*, 1–165. http://doi.org/10.2737/IITF-GTR-39

Grau HR, Aide TM, Zimmerman JK, et al (2003) The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. Bioscience 53:1159–1168. doi: 10.1641/0006-3568(2003)053[1159:TECOSA]2.0.CO;2

Helms KR, Vinson SB (2003) Apparent facilitation of an invasive mealybug by an invasive ant. Insectes Sociaux 50:403–404. doi: 10.1007/s00040-003-0702-4

Hengeveld R (1989) Dynamics of Biological Invasions. Springer Science & Business Media

Holle Von B, Simberloff D (2005) Ecological resistance to biological invasions overwhelmed by propagule pressure. Ecology 86:3212–3218. doi: 10.1890/05-0427

Isenmann P (1990) Some recent bird invasions in Europe and the Mediterranean Basin. In: Biological Invasions in Europe and the Mediterranean Basin. Springer Netherlands, Dordrecht, pp 245–261

Janzen DH (1981) *Ficus ovalis* seed predation by an orange-shinned parakeet (*Brotogeris jugularis*) in Costa Rica. Auk 98:841–844.

Juniper T, Parr M (1998) Parrots: a guide to the parrots of the world.

Kleunen A, Bremer L, parakeet RLTR-R, 2010 (2010) The rose-ringed parakeet, monk parakeet and Alexandrine parakeet in the Netherlands: risk analysis and management.

Luque GM, Bellard C, Bertelsmeier C, et al (2013) The 100th of the world's worst invasive alien species. Biol Invasions 16:981–985. doi: 10.1007/s10530-013-0561-5

Moulton MP, Pimm SL (1986) Species introductions to Hawaii. In: Mooney HA, Drake JA (eds) The ecology of biological invasions of North America and Hawaii. New York, pp 231–249

Nebot JC (1999) First report on the rose-ringed parakeet (*Psittacula krameri*) in Venezuela and preliminary observations on its behavior. Ornitología Neotropical 10:115–117.

Oberle MW (2000) Puerto Rico's Birds in Photographs. Editorial Humanitas, San Juan

Pérez-Rivera RA, Colón Méndez G, Ríos Estrella W, de Jesús Suárez WL (1985) Aspectos de la ecología del periquito de ala amarilla (*Brotogeris versicolurus*) en Puerto Rico. Science-Ciencia 12:1–5.

Pimm SL (1989) Theories of predicting success and impact of introduced species. In: Drake JA, di Castri F, Groves RH, et al. (eds) Biological invasions. John Wiley & Sons Incorporated, pp 351–367

Pimm SL, Jones HL, Diamond J (1988) On the Risk of Extinction. The American Naturalist 132:757–785. doi: 10.1086/284889

Pithon JA, Dytham C (1999) Census of the British ring-necked parakeet *Psittacula krameri* population by simultaneous counts of roosts. Bird Study 46:112–115. doi: 10.1080/00063659909461121

QGIS Development Team (2017) QGIS Geographic Information System. https://www.qgis.org/

R Core Team (2017) R: A language and environment for statistical computing. http://www.R-project.org

Raffaele HA (1989) A Guide to the birds of Puerto Rico and the Virgin Islands. Princeton University Press.

Robinet O, Salas M (2008) Reproductive biology of the endangered Ouvea Parakeet Eunymphicus cornutus uvaeensis. Ibis 141:660–669. doi: 10.1111/j.1474-919X.1999.tb07374.x

Russello MA, Avery ML, Wright TF (2008) Genetic evidence links invasive monk parakeet populations in the United States to the international pet trade. BMC Evolutionary Biology. doi: 10.1186/1471-2148-8-217

Sakai AK, Allendorf FW, Holt JS, et al (2001) The population biology of invasive species. Annual Review of Ecology and Systematics 32:305–332. doi: 10.1146/annurev.ecolsys.32.081501.114037

Schroads CV (1974) Studies in a population of the canary-winged parakeet, *Brotogeris versicolurus* (PLS Müller) in Dade County, Florida (Aves: Psittacidae). University of Miami

Sol D (2008) Do successful invaders exist? Pre-adaptations to novel environments in terrestrial vertebrates. In: Biological Invasions. Springer, Berlin, Heidelberg, pp 127–141

Strubbe D, Matthysen E (2011) A radiotelemetry study of habitat use by the exotic Ring-necked Parakeet Psittacula krameri in Belgium. Ibis 153:180–184.

Sullivan BL, Phillips T, Dayer AA, et al (2017) Using open access observational data for conservation action: A case study for birds. Biological Conservation 208:5–14. doi: 10.1016/j.biocon.2016.04.031

Tossas AG, Colón YM, Sanders I (2012) Seasonal changes in roost counts of the non-native white-winged parakeet (*Brotogeris versicolurus*) in San Germán, Puerto Rico. Journal of Caribbean Ornithology 25:1–6.

van Bael S, Pruett-Jones S (1996) Exponential population growth of Monk Parakeets in the United States. Wilson Bulletin 108:584–588.

Veit RR (1997) Long-distance dispersal and population growth of the yellow-headed blackbird *Xanthocephalus xanthocephalus*. Ardea 85:135–143.

Veit RR (2000) Vagrants as the expanding fringe of a growing population. Auk 117:242–246.

Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer.

Wunderle JM (1994) Census methods for Caribbean land birds. Gen. Tech. Rep. SO-98, 1–26. Southern Forest Experiment Station.

TABLES

Table 1: Population estimates and growth rates (λ) of the white-winged parakeet (*Brotogeris versicolurus*) at two sites in Puerto Rico. Counts were performed during the non-breeding season (N_{nb})

Year	San Patricio		San Germán	
	N_{nb}	λ	N_{nb}	λ
1975	–	–	200*	–
1981	360*	–	–	–
1995	–	–	800#	1.07
2005	–	–	1,335†	1.05
2007	1,299	1.05	1,503	1.13
2008	2,301	1.77	1,779	1.18
2009	3,128	1.36	2,406	1.35
2010	2,531	0.81	3,010	1.25

Table 2: Breeding proportion of the population based on the 2010 breeding (*Nb*) and non-breeding season counts at the roosting site, the estimated number of pairs, expected chick production and the estimated number of fledglings.

Population	N_b	Breeding prop.	No. of pairs	Chicks	Fledglings
San Patricio	1,879	0.40	625	1,250	604
San Germán	1,382	0.42	512	1,024	–

Table 3: Plant resources used by the white-winged parakeet (*Brotogeris versicolurus*) for food and nesting in Puerto Rico. Information based on observations made during the study period, with additional information from Pérez-Rivera et al. (1985).

Species	Common name	Status	Resource used
			Food resources
Albizia procera	White siris	Invasive	sap
Annona muricata	Soursop	Exotic	fruits
Artocarpus heterophyllus	Jackfruit	Exotic	flowers
Bucida buceras	Bullet tree	Native	flowers, seeds
Callistemon citrinus	Lemon bottlebrush	Exotic	flowers, nectar
Carica papaya	Papaya	Exotic	fruits
Cassia javanica	Pink shower tree	Exotic	flowers
Cassuarina equisetifolia	Australian 'pine'	Invasive	seeds
Cecropia peltata	Trumpet tree	Native	fruits
Ceiba pentandra	Kapok	Native	flowers
Citrus paradisi	Grapefruit	Exotic	fruits
Clusia rosea	Autograph tree	Native	seeds
Cocos nucifera	Coconut palm tree	Exotic	flowers, nectar?
Cordia sebestena	Scarlet cordia	Native	flowers, nectar?
Delonix regia	Royal poinciana	Exotic	flowers
Erythrina poeppigiana	Coral tree	Exotic	shoots
Ficus americana	West Indian fig	Native	fruits
Ficus citrifolia	Shortleaf fig	Native	fruits

Inga vera	Guaba	Native	seeds
Malpighia emarginata	Barbados cherry	Native	fruits
Mangifera indica	Mango	Exotic	flowers, fruits
Musa acuminata	Banana	Exotic	fruits
Musa paradisiaca	Plantain	Exotic	fruits
Ochroma pyramidale	Balsa	Exotic	seeds
Pithecellobium dulce	Manilla tamarind	Exotic	flowers, seeds
Psidium guajava	Guava	Exotic	fruits
Pterocarpus officinalis	Dragonsblood tree	Native	flowers
Roystonea borinquena	Royal palm	Native	fruits
Spathodea campanulata	African tulip tree	Exotic	flowers, seeds
Spondias mombin	Yellow mombin	Exotic	fruits
Spondias purpurea	Red mombin	Exotic	fruits
Sterculia apetala	Panama tree	Exotic	seeds
Swietenia mahogani	West Indian mahogany	Exotic	seeds
Syzygium jambos	Water apple	Exotic	fruits
Tabebuia heterophylla	Pink trumpet tree	Native	flowers, seeds
Terminalia catappa	Indian almond	Exotic	fruits
Zanthoxylum martinicense	Prickly ash	Exotic	shoots
			Roosting resources
Callophyllum antillanum	Antilles calophyllum	Native	–

Roystonea borinquena	Royal palm	Native	–
Eucalyptus deglupta	Rainbow eucalyptus	Exotic	–
Swietenia mahogani	West Indian mahogani	Exotic	–
			Nesting resources
Albizia procera	White siris	Exotic	termite mounds
Artocarpus heterophyllus	Jackfruit	Exotic	termite mounds
Cordia sulcata	White manjack	Native	termite mounds
Delonix regia	Royal poinciana	Exotic	termite mounds
Dendropanax arboreus	Angelica tree	Native	termite mounds
Ficus citrifolia	Shortleaf fig	Native	termite mounds
Mangifera indica	Mango	Exotic	termite mounds
Pithecellobium saman	Albizia saman	Exotic	termite mounds
Schefflera morototoni	Yagrumo macho	Native	termite mounds
Spondeas mombin	Yellow mombin	Exotic	termite mounds
Swietenia macrophylla	Honduran mahogani	Exotic	termite mounds
Swietenia mahogani	West Indian mahogani	Exotic	termite mounds
Tamarindus indica	Tamarind	Exotic	termite mounds
Terminalia catappa	Indian almond	Exotic	termite mounds
Zanthoxylum martinicense	Prickly ash	Native	termite mounds

FIGURES

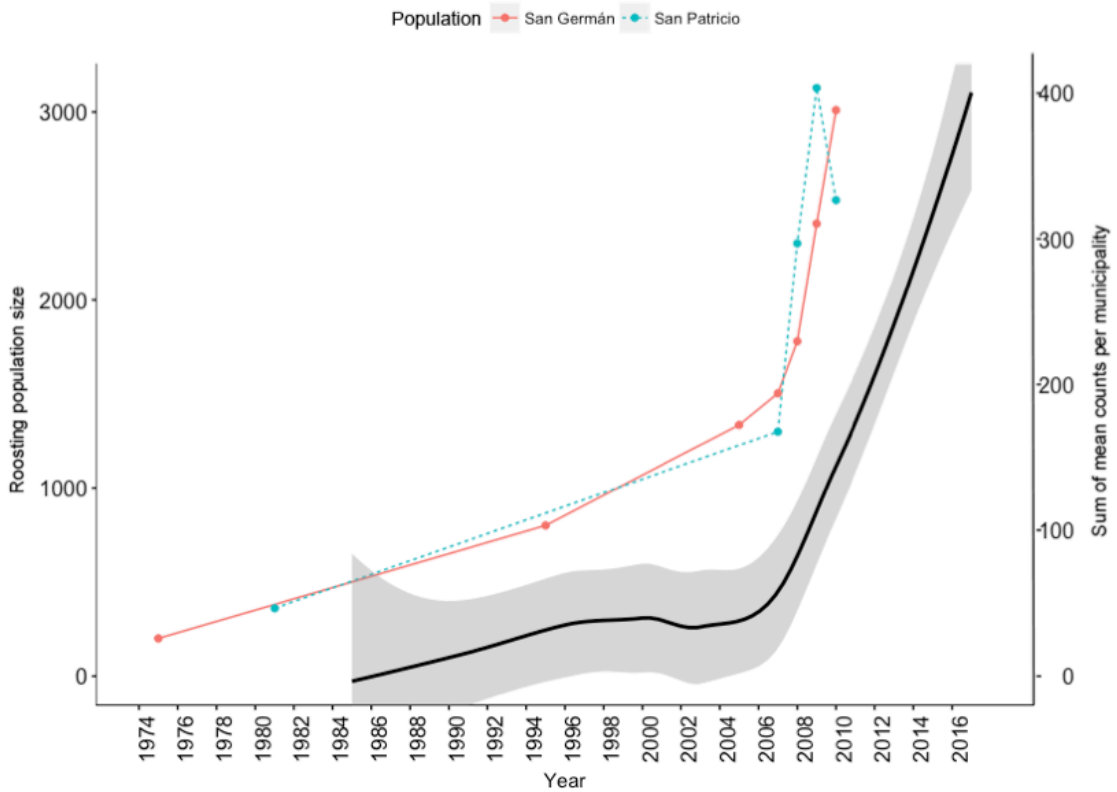

Figure 1: Island-wide population increase of the white-winged parakeet (*Brotogeris versicolurus*) in Puerto Rico (black line) and population increase in two populations (roosting sites) over the years. Island-wide population increase was calculated as the sum of the mean number of birds counted per year/municipality (data from *Ebird*). Grey shading indicates the 95% CI based on the local weighted scatterplot smoothing (loess).

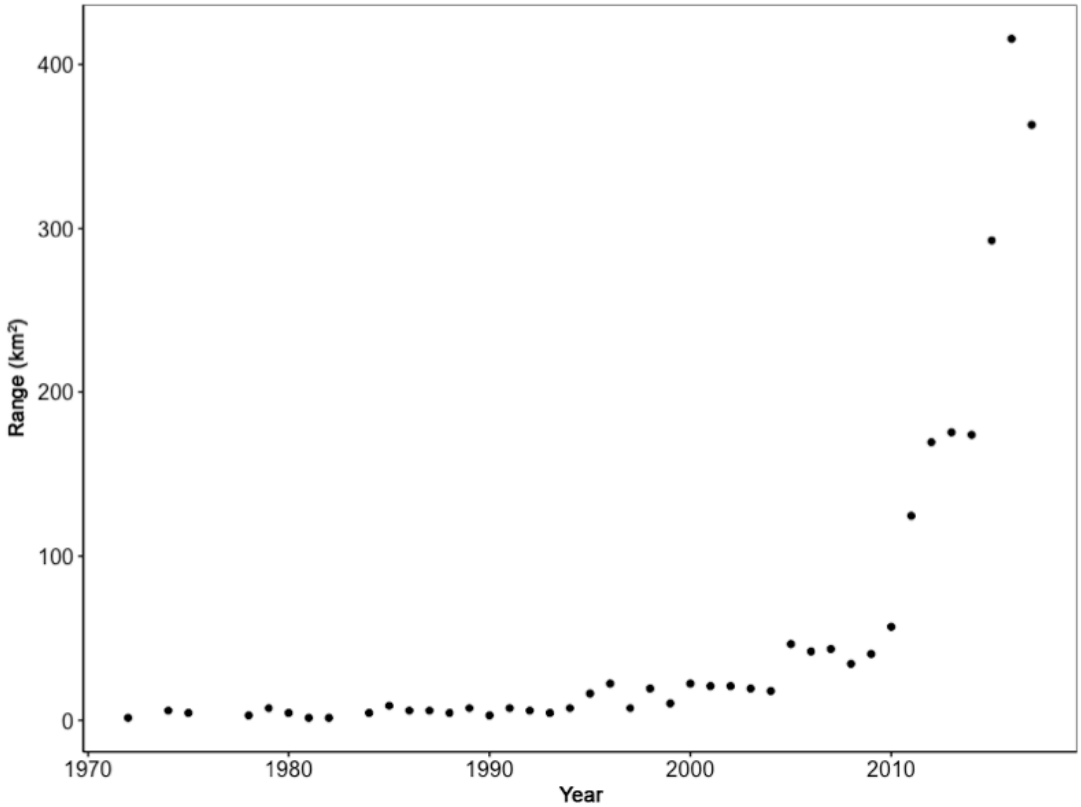

Figure 2: Island-wide geographic range expansion of the white-winged parakeet (*Brotogeris versicolurus*) in Puerto Rico over the years. Island-wide range expansion increase was calculated using sighting data from *Ebird* (see methods).